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The Behavior of *Euxenister* and *Pulvinister*, Histerid Beetles Associated with Army Ants

(Coleoptera : Histeridae; Hymenoptera : Formicidae : Dorylinae)[1]

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Most ecitophilous beetles belong to the families Histeridae, Limulodidae, and Staphylinidae, with the latter two being by far the most abundant. However, about 20 species of distinctly myrmecophilous histerids have been collected with army ants (Rettenmeyer, 1961). This excludes histerids found only in refuse deposits, and those listed in primarily taxonomic papers with little more than host data given, making the histerids affinity with the ants somewhat uncertain. Discussion in this paper will be limited to the two most common and conspicuous genera, *Euxenister* and *Pulvinister*, since both field and laboratory data were collected on their behavior.

All literature on ecitophilous histerids is taxonomic with the exception of Rettenmeyer (1961) who includes excellent field and laboratory observations on *Euxenister*, *Pulvinister*, and several other genera. Methods of collecting and studying army ants and their guests, keeping guests alive in laboratory nests, and designation of colonies by number have been elaborated in a previous paper (Akre and Rettenmeyer, 1966).

All histerids in this study were collected during 1 March–9 May 1963 and 6 February–3 June 1967 at the Smithsonian Tropical Research Institute (Barro Colorado Island), Canal Zone. Although primarily a field study, considerable data were gathered on these histerids in laboratory nests.

Euxenister caroli Reichensperger

Euxenister caroli is a robust histerid with several structural modifica-

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tions for living with army ants (Reichensperger, 1924). The most conspicuous is the long hind legs that allow it to keep pace with army ants when they emigrate during their nomadic phase. The legs are further adapted in that the tibia are grooved distally and the tarsi can be folded into this groove when danger threatens, thereby preventing removal. The head can be retracted into the pronotum and the antennae are then covered by the lateral carinae of the pronotum. The entire surface of the body is heavily sclerotized and with all appendages drawn flush to the body surface, the beetle is nearly immune to damage by ants. In addition, the pronotum and the elytra have lateral carinae making them quite rigid.

Euxenister caroli has been found only with *Eciton burchelli* (Westwood). Fifty *E. caroli* were collected from emigration columns of 11 colonies while several more were seen but not collected. The number in any one colony varied from 1–9, the average being 4.5. Twenty-six *E. caroli* were seen running in columns, the rest were riding army ants or larvae or booty. In one instance, a *Euxenister* running in the column had a minor worker of *Eciton* grasping its mandibles to the right lateral carina of the beetle. The worker being small, its legs frequently did not touch the substrate, leaving the impression it was riding the histerid. The remaining histerids rode in a number of different positions, but the most frequent was on the posterior end of a larva or piece of booty that extended beyond the gaster of the worker carrying it. Eighteen *Euxenister* were collected riding in this position. One histerid rode under the thorax and head of a minor worker which consequently had great difficulty walking along the column. The remaining 5 histerids were riding under the thorax and anterior to the first coxae of workers. Three were on intermediate workers and 2 on submajors. All 4 of these ants were carrying several small larvae, and the histerids may have been holding to these larvae; but apparently they were holding directly to the thorax of the ants. In all cases except where *E. caroli* was riding on very large larvae or booty, the histerids rode upside down facing forward.

The characteristic behavior of *E. caroli* in laboratory nests was a frequent "grooming" of the workers. This was usually confined to major workers, but the histerid also groomed submajors and large intermediates (Rettenmeyer, 1961:496). I observed similar behavior in nests supplied with workers of all sizes including 5–10 majors. If the major workers died, histerids started grooming intermediates and even groomed minor workers smaller than themselves when few or no

larger workers were present. Occasionally histerids groomed minor workers when at least 5 majors were present.

While grooming a worker, *E. caroli* most frequently climbed on top of the thorax of the worker and faced forward (fig. 1). The histerid's prothoracic legs rested on the ant's head; the mesothoracic legs were placed in front of the anterior coxae of the worker; and the metathoracic legs were placed along the sides of the ant's thorax with the tarsi resting on the ant's meso- and metathoracic legs. In this position the histerid licked the ant's head and antennae with its maxillae and simultaneously rubbed the ant's body with its legs.

Euxenister caroli has dense long hairs on the inner surface of the distal one-fourth to one-third of each tibia. These "tibial brushes" were the principal parts of the legs rubbed against the worker's body. The mesothoracic legs rubbed most vigorously and most frequently rubbed the area in front of the worker's front coxae. The prothoracic legs rubbed slowly and alternately on top of the worker's head; and the metathoracic legs were used mostly for grasping, or for slowly rubbing the sides of the ant's thorax.

The tarsi were usually retracted into grooves in the tibiae when the histerid was rubbing. Since a histerid sometimes used all legs to rub an ant, it frequently became unbalanced. In this case the prothoracic tarsi were extended, and the tarsal claws grabbed the surface of the ant's head. The histerid frequently left its tarsi extended for a minute or more even after it started rubbing the ant's head again with its front legs.

At frequent and irregular intervals the histerid stopped rubbing the ant and rubbed its legs on its own body for 2 or 3 strokes. The mesothoracic legs were rubbed on trichomes of the dorsolateral carinae of the elytra, and the metathoracic legs were rubbed on the numerous trichomes on the end of the abdomen. The tibiae, including the tibial brushes, were the main parts rubbed against the histerid's body. The front legs were occasionally rubbed only on the histerid's head and pronotum.

Reichensperger (1924:130–131) reported masses of glands plus large individual glands in the prothorax of *E. caroli* discharge through secretory ducts that open through pores to the surface. He suggested these glands secrete an "agreeable" fatty substance. In an earlier paper Reichensperger (1923:335–336) considered hairs on the elytra and prothorax of *E. caroli* to be trichomes which are highly attractive to the ants. Seyfried (1928:26–27) found that the socket of each hair of *Chrysetaerius iheringi* Reichensperger had an opening of a duct from

a modified hypodermal gland. *Chrysetaerius iheringi* has "special thick combs" of these glandular hairs (trichomes) on the inner surfaces of the tibiae of the middle and hind legs. Although Seyfried made no histological study of *E. caroli*, he assumed that all long hairs of myrmecophilous histerids are symphilic trichomes. He also suggested (op. cit., p. 57) the trichomes were covered with a fatty substance that "charmed" the ants while they carried a histerid.

Rettenmeyer (1961:497–498) suggested that the fatty substance on the tibial brushes of *E. caroli* may transfer colony odor from the ant to the body of the histerid, and that this may be one reason why the histerid rubs both the ant and itself with its legs. This odor may prevent ants from attacking a histerid. He also suggested that trichomes along the dorsolateral carinae may rub this chemical odor off the histerid's legs.

Workers of *E. burchelli* did groom *E. caroli*; but at no time did I observe any particular attraction of the ants to trichomes on the legs, prothorax, or abdomen. If the tibial brushes were an adaptation to "charm" the ants they would be on the outer rather than the inner edge of the tibiae (Rettenmeyer, 1961:498). For these reasons it seems more likely these hairs on *E. caroli* transfer colony odor from the ants to the body of the histerid rather than being trichomes. In addition, if these "trichomes" were really highly attractive to *E. burchelli*, they possibly would also have been, but were not, attractive to *Eciton hamatum* Fabricius.

The rate of rubbing of the worker by *E. caroli* seemed related to the degree of excitation of the ants. Rettenmeyer (1961:499) reported some inconculsive evidence that rubbing by the histerid decreased the vigor of the ant's attack. I observed that when the ants were excited, the histerid rubbed a worker very rapidly which seemed to calm it. Many times workers that *E. caroli* was grooming started moving as if trying to escape, but the histerid then rubbed more vigorously until the ant became still. Often the ant being rubbed appeared paralyzed or incapable of movement, even when the weight of the histerid caused the ant to fall over backwards or sideways. The ant remained in that position while the histerid groomed it. Once an *E. caroli* was rubbing a small intermediate worker and licking its antennae when they fell over. The worker lay on its back on top of the histerid while the beetle continued to rub the ant's prosternum with its mesothoracic legs. As the histerid licked the ant's antennae, the ant remained immobilized with legs slightly curled and twitching spasmodically. After about 30 seconds the *Euxenister* shifted its position slightly and licked the man-

dibles of the worker; but the worker turned over and ran away causing the histerid to fall.

Similar behavior was frequently observed when the worker tipped over backwards on its petiole as the histerid was grooming. The head and thorax of the ant were nearly perpendicular to the floor, with the gaster doubled under nearly parallel to the thorax. The *E. caroli* stayed on the ant and continued to rub and groom it. Except for slight twitching of the legs, these ants remained motionless for up to several minutes.

Whenever a histerid maintained its position on an ant's thorax, it cleaned or licked the ant's antennae. Licking was restricted primarily to the scape, perhaps because the *Euxenister* could not reach farther without falling off. However, several times a histerid managing to bend back the ant's antennae with its front legs cleaned the flagellum also. The maxillae moved rapidly over the surface of an antenna lying between its mandibles. The mandibles moved slightly but were always open enough to not clamp the antenna. The labial mouth parts sometimes moved, but it was difficult to see whether they also cleaned the antennae. After antennae were licked, the histerid usually licked around the mandibles and top of the ant's head.

In addition to cleaning the worker's antennae and head, *E. caroli* licked the thorax, gaster, and legs less frequently. It rubbed the ants while licking these parts also. *Euxenister caroli* sometimes licked the mandibles of a major worker, and then walked down the mandibles until it was upside down facing backwards under the major's head. The histerid's legs were hooked over the top of the major's head, and in this position the beetle rubbed more slowly than when on top of the ant. Although *E. caroli* crawled all over an ant's head and between its mandibles, even to the point of sticking its legs on the ant's maxillae; no ant was seen to bite the histerid.

Euxenister caroli spent nearly all its time in the nests grooming the ants for periods averaging 3 minutes per worker for 61 observations. The 4 longest times observed grooming a worker were 13 minutes 25 seconds, 7 minutes, 5 minutes, and 4 minutes 35 seconds. The histerid never seemed to rest but continuously moved from worker to worker.

Euxenister caroli was seen several times in mouth-to-mouth trophallaxis with army ant workers. One *E. caroli*, collected on 24 March, was placed in a laboratory nest containing 20 workers from its host colony on 26 March. The histerid went straight into the cluster of ants. One worker was chewing on a piece of booty (nondoryline ant larva) and the histerid started chewing on the free end. It stopped after a few seconds and puts its mouth parts against the mouth parts

of an intermediate worker. This contact was broken within a few seconds. After drinking water from the moist dirt in the nest, the histerid grabbed the maxillae or labium of a submajor worker and started pulling. I was unable to determine what mouth parts the histerid was using except it was not mandibles. The submajor reared back on its gaster, pushed, and struck the beetle with its front legs, but did not dislodge it. A drop formed between the ant's mandibles, and the histerid drank this fluid. When the beetle released the ant after about 10 seconds, the area between the ant's mandibles was still covered with fluid. The histerid climbed on the head of another submajor and tried to get to its mouth parts; but the ant became excited and shook off the beetle. Later, another *E. caroli* and a worker were seen with their mouth parts touching. The histerid seemed to be pulling vigorously on the labium of the worker. After a few seconds, the histerid moved to another worker. The ant and histerid had their mouth parts together, but there was no pulling; and no exchange of fluid could be seen. This same *E. caroli* and an intermediate worker were observed 2 days later with mouth parts together and moving rapidly, but no exchange of fluid was seen. Although workers licked the mandibles of *E. caroli* on numerous occasions, no further observations were made on mouth-to-mouth trophallaxis. Since the histerids were observed for more than 50 hours trophallaxis must have been infrequent.

Euxenister caroli frequently ate army ant brood and booty (fig. 2). It has very efficient mandibles and was more effective than ants in cutting open larvae and booty. When some *E. burchelli* brood was put in one of the nests, the histerid immediately cut a hole in a larva causing liquid to ooze. The *E. burchelli* workers pushed one another out of the way to get at the juices. The ants became so numerous that the beetle was pushed completely away from the larva. The mouth parts of the beetle were still wet, and 3 minor workers successively licked them. Two *E. caroli* in another nest cut holes in an ant pupa (booty), and the ants immediately crowded in from both sides to lick the oozing fluid. By pushing the beetles out of the way, the ants caused them to cut holes in many more army ant larvae or pieces of booty than the beetles could eat. *Euxenister caroli* may be detrimental to the army ants by eating both brood and booty. Rettenmeyer (1961:502) suggested cannibalism of army ant broods by the workers may be initiated by histerids or other myrmecophiles.

Euxenister caroli was not licked or cleaned frequently by the ants. Grooming took place immediately after the histerid was introduced into the nest or after the beetle had fed. For example one *Euxenister*, follow-

ing its introduction into a nest, began to groom a submajor while a minor worker licked the histerid's elytra between the dorsolateral carinae; and 3 other workers cleaned the beetle's legs. Workers were observed grooming specimens of *E. caroli* only 4 more times; three times workers licked the histerid's mandibles, pronota, and between the dorsolateral carinae, and the last time a minor worker licked the head and next the histerids' abdomen. Ants at no time concentrated their grooming on the "trichomes."

Since *E. caroli* is host specific to *E. burchelli,* it was usually placed in laboratory nests with workers of its host. After observations had been made the *E. burchelli* workers were replaced with 5 majors and 20 other workers of *E. hamatum* per nest. When the *E. caroli* that had been in this nest with *E. burchelli* workers was put back in the nest, an intermediate *E. hamatum* worker grabbed the beetle's hind leg. Another intermediate seized the dorsolateral carina of the pronotum. The histerid walked and dragged workers whenever the ants let its legs touch the ground. Although the histerid was continuously attacked and often dragged around the nest for 30 minutes, at no time did it retract its legs. After this treatment, a careful examination revealed no injuries; and the histerid was returned to the nest on 6 April. On 8 April the histerid was seen eating some *E. hamatum* brood that had been placed in the nest for food. A few minutes later an intermediate worker picked up the histerid by one carina of the pronotum and dropped the beetle in a refuse deposit in one corner of the nest. Up to this time the *Euxenister* had stayed along the outer edges of the nest and seemed to avoid the ants. On 14 April this histerid was seen grooming workers, concentrating its efforts on the 5 majors in the nest. When the histerid was first seen it was upside down, facing posteriorly on the gaster of a major. It was furiously rubbing the top of the major's gaster with all 3 pairs of legs. The mesothoracic legs rubbed most actively, followed by the prothoracic legs. The metathoracic legs rubbed only occasionally while clinging to the worker. The histerid left this major, crawled up on the thorax of another and licked the top of its abdomen while facing posteriorly. When the histerid dismounted, a minor worker bit the beetle's leg but released it in less than ½ minute. During the next 5 days, the histerid intermittently groomed majors and was attacked from time to time by smaller workers. It was uninjured when examined on 19 April.

In summary, one specimen of *E. caroli* was still attacked by *E. hamatum* workers after being in a laboratory nest with them for 13 days. During much of this time it was grooming and rubbing *E.*

hamatum workers and should have acquired some of the odor of this species. The strong odor of the *Euxenister caroli* itself or of the *Eciton burchelli* may have caused the attacks. The *E. hamatum* workers were never seen grooming the *E. caroli* and were not attracted to the histerid's "trichomes."

EUXENISTER WHEELERI Mann

Euxenister wheeleri is very similar to *E. caroli* in having long hind legs, retractable head and antennae, and grooves on the tibia for the tarsi. However, the lateral carinae are not so pronounced and the histerid is somewhat less sturdy (fig. 4).

Seventy-five *Euxenister wheeleri* were collected, all from emigration columns of 13 colonies of *Eciton hamatum* with which it is host specific. The number of histerids per colony varied 1–16, the average 5.77. Fifty-three were running in columns (fig. 3), one was collected in a sample of ants from the bivouac, and the remainder were riding on brood or booty in the manner of *E. caroli.* Nine rode in an undetermined position on the posterior ends of booty; 9 rode upside down facing forward on posterior ends of larvae, one rode facing forward on the side of a larva; one rode facing forward on a large membranous wing carried as booty; and one rode on the gaster of a male *E. hamatum.*

When an *Euxenister wheeleri*, previously in an *E. burchelli* laboratory nest for 16 hours, was released at the edge of a raid column the beetle was briefly attacked as it ran 10 cm toward the bivouac. Then the beetle turned to face the oncoming ants and grasped the body of a wolf spider being carried as booty. Rettenmeyer (1963) observed similar reversals of running in *Trichatelura manni* (Caudell) apparently trying to catch rides on booty or brood.

The behavior of *E. wheeleri* closely paralleled that of *E. caroli*, but in several aspects was either totally different or less intense and this discussion is concentrated on these differences. *Euxenister wheeleri* was similarly attracted to and groomed major and large intermediate workers. Although it varied its position while grooming, one position was assumed by the histerid slightly more frequently than any other. The histerid crawled under, and hooked its legs over, the major's head. It usually faced posteriorly and crawled gradually down the entire underside of the ant licking and cleaning as it progressed. The coxae, and infrequently the proximal ends of the femora, were licked. This anterior to posterior pattern was observed 15 times and 6 times the histerid was faced anteriorly.

FIG. 1

FIG. 2

FIG. 3

FIG. 4

FIG. 5

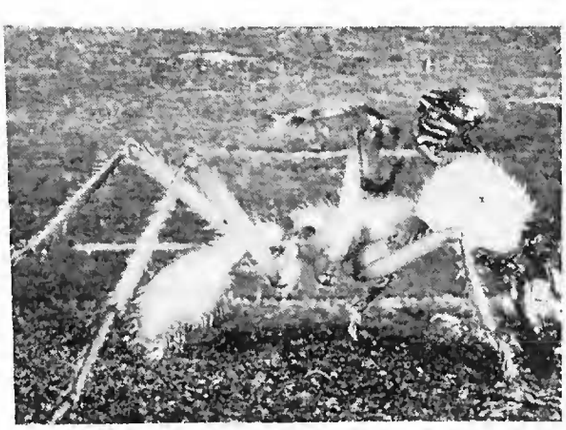

FIG. 6

FIG. 1. *Euxenister caroli* in typical grooming position on major of *Eciton burchelli.* FIG. 2. *E. caroli* feeding on a larva of *E. burchelli.* FIG. 3. *Euxenister wheeleri* running in an emigration column of *Eciton hamatum.* The exceptionally long legs enable it to keep pace with the ants. FIG. 4. *E. wheeleri* grooming an *E. hamatum* major. FIG. 5. *Pulvinister nevermanni* riding between the mandibles of an *E. hamatum* major. FIG. 6. A *P. nevermanni* riding on an *E. hamatum* major attached only by its front legs.

Euxenister wheeleri has brushes on all tibiae similar to those of *E. caroli.* These brushes were rubbed on the ant's body much more slowly than *E. caroli.* The meso- and metathoracic legs were used about equally in rubbing and seemed to rub alternately one leg at a time, rather than simultaneously. The middle and hind legs, but never the front legs, were rubbed on its own body in the same places as *E. caroli.* This histerid rubbed the ant before it rubbed itself.

In contrast with *E. caroli,* the rubbing by *E. wheeleri* did not tranquilize or paralyze their ant hosts. This is probably not necessary as *E. hamatum* is not normally as excitable as *E. burchelli.* Sometimes the histerid completely licked a major worker without rubbing it. The histerid frequently rubbed so slowly that it was impossible to distinguish between rubbing and shifting of body position. *E. wheeleri* never increased its rate of rubbing when the ant started to move.

Both species of *Euxenister* licked and rubbed workers while on top of them, but *E. wheeleri* more frequently hung underneath the ant. *Euxenister wheeleri* spent less time than *E. caroli* on the heads of major workers, and was observed about 5 times on the top of the head of an *E. hamatum* major licking its head and antennae. *Euxenister wheeleri* seemed to have a greater preference than *E. caroli* for major workers, sometimes grooming submajors and large intermediates but never smaller workers.

Euxenister wheeleri was observed with mouth parts against those of a worker only 4 times (one minor and 3 intermediate workers). Twice this may have been ants cleaning the beetle's mouth parts since the histerid had just fed. The other 2 times the histerid and worker stayed together for 20–25 seconds. No fluid was seen to suggest trophallaxis, but possibly trophallaxis occurred.

The histerids fed on large amounts of *E. hamatum* and *E. burchelli* larvae and booty in the nests. One *Euxenister* devoured 3 live *E. hamatum* larvae about 5 mm long and next began to feed on a large ant pupa (booty). *E. wheeleri* also chewed holes in more brood and booty than necessary for food since the ants always pushed the histerid away from its feeding site. One *E. wheeleri* chewed 5 holes in the gaster of a polybiine wasp pupa because the workers pushed it away to get at the juices. Although 4 other pieces of booty were in the nest, the workers fed on the pupa the histerid had cut open.

Euxenister wheeleri was observed being licked by workers only 5 times, including once when 4 workers simultaneously groomed one histerid. The workers licked the head, prothorax, elytra, legs, and abdomen, showing no preference for trichomes. In some of the nests

with as many as 6 *E. wheeleri*, the histerids licked the sides and end of the abdomen of each other.

Only once was an *E. wheeleri* attacked by the workers of *E. hamatum*. A histerid from one colony placed in a laboratory nest with workers of another was immediately attacked by a minor worker and soon pinned down by others. Then an intermediate worker picked the histerid up by the dorsolateral carina of the pronotum, carried it to a corner of the nest and dropped it. The histerid was attacked for a few seconds several more times. Within 14 minutes after its introduction into the nest, the histerid was busy grooming a major and was not attacked again.

PULVINISTER NEVERMANNI Reichensperger

Pulvinister nevermanni is smaller than *Euxenister* but has similar pronotal carinae and grooves on the tibia to receive the tarsi.

Forty-three *Pulvinister*, host specific to *E. hamatum*, were taken riding on ants or larvae in emigrations. Twenty were on the posterior ends of larvae, 19 rode at the bases of mandibles of majors (fig. 5), one was carried between the mandibles of an intermediate worker, and one walked in the column. Ten additional *P. nevermanni* were collected among large samples of *E. hamatum* workers, brood, and booty in bivouacs.

Pulvinister nevermanni always rode under the heads of major workers during emigrations and in laboratory nests (Rettenmeyer, 1961:512). I observed the histerid climb up the major's mandibles, front legs, or over the top of its head to get to this position. The ants never picked up the histerid and a *Pulvinister* was seen being carried only once during an emigration. When 10 majors were placed in a laboratory nest with 5 *P. nevermanni*, the majors ran excitedly about the nest. Several histerids fastened onto the abdomens of majors and rode, but while the others constantly tried, they did not succeed. While the histerid could mount the abdomen of a major that was running at full speed, apparently a major must be still for a histerid to get under its head. After 1.5 hours, when 40 smaller workers were placed in the nest, the majors stood still while the workers groomed them and the histerids got into position under the majors' heads by crawling up the majors' mandibles. In this position the histerid usually held on only by front tarsal claws clasped onto hairs on the undersurface of the ant's head. The middle and hind legs were retracted tightly against the histerid's body. The histerid was always close to the base of the major's mandibles, appearing sometimes as though a major carried

the histerid (see Rettenmeyer, 1961:512). The histerid nearly always rode hanging onto the major with only the front legs, but the beetle sometimes grabbed hairs with mesothoracic tarsal claws, especially when other workers bumped into the histerid in grooming the major.

While in this characteristic position, *P. nevermanni* usually remained quiet but several times was seen licking and cleaning the bases of the major's mandibles. Majors were also observed to often lick the undersurface of the histerids. I thought a gland might have an opening in the base of the major's mandible, but no pore was seen in a mandible cleared in potassium hydroxide.

When under an ant's head, *P. nevermanni* irritated the ant, judging from majors' frequently kicking at the beetles with their front legs and bending the gaster forward attempting to sting the beetles. However, only when the beetle had not yet settled in position could it be dislodged. It also irritated intermediate and smaller workers which were successful in dislodging the histerid from any position on their bodies. This is probably why *Pulvinister* most frequently rides between the mandibles of majors. The histerid also seemed to interfere with the ant's feeding. One major spread its mandibles over a piece of booty and tried to feed but could not because the histerid was in the way. The major immediately reared its body upward and back on its gaster and kicked at the histerid with its front legs. After about one minute the major stopped kicking, but the histerid had moved only slightly. The ant then spread its mandibles and pushed its mouth parts down hard on the booty. The histerid was pressed between the ant's head and the booty and finally moved out of the way, allowing the major to feed.

Pulvinister nevermanni usually folded its legs against its body and pulled its head back into the prothorax whenever bumped by a worker. Unlike *Euxenister* spp., it did not stand up with its front legs outstretched. Although the histerid was not attacked by the ants in the laboratory nests, it frequently assumed this essentially invulnerable position when "jostled" by the ants.

In addition to the typical position under the heads of majors, *Pulvinister nevermanni* also rode on ants in laboratory nests in various other positions on majors such as the top of heads, the distal ends of crossed mandibles, and on various positions on the ant's gaster. Most frequently the histerid was found on top of the gaster clinging only by its front tarsal claws while the other legs were folded tightly against its body. The histerid protruded very conspicuously in this position (fig. 6), and rode for as long as 4 hours.

Unlike *Euxenister* spp., *P. nevermanni* groomed ants at infrequent intervals. The histerid was seen licking the thorax of an intermediate worker once, the legs of a major once, and the head and antennae of a major several times. However, when *Pulvinister* did groom workers, its behavior was similar to *Euxenister*. It rubbed its middle and hind legs slowly on the surface of the ant and then the mesothoracic legs alternated in rubbing on the outside of the hind legs; the hind legs in turn alternated in rubbing on the end of the histerid's abdomen. *Pulvinister* has tibial brushes, similar to but not as dense as those of *Euxenister,* which it rubs against the body. However, *Pulvinister* has no hairs on the end of its abdomen to receive any odor that may be transferred in this manner. Other than this infrequent grooming behavior, *Pulvinister nevermanni* spent all of its time in nests riding on majors, feeding, buried in booty or brood, or buried under soil. Sometimes it remained buried for two or three days.

Trophallaxis may occur when *P. nevermanni* rides under a major's head, but this position prevented observation. Excluding the riding histerids, *P. nevermanni* and a major were observed in mouth-to-mouth contact only once. The major was dying and was over on its back though still able to move. When the histerid placed its mouth parts against those of the ant both insects moved their mouth parts rapidly but no exchange of fluid was seen.

Pulvinister nevermanni fed like the *Euxenister* spp. on army ant brood and booty. When 100 small *Eciton hamatum* larvae were added to a nest with 5 *Pulvinister* and approximately 40 ants, the histerids immediately chewed holes in the larvae. As the beetles were pushed out of the way by workers competing for the oozing juices, the histerids attacked additional larvae until about half were dead or dying within an hour. The ants and histerids had not been fed for 2 days and probably were more voracious than usual. The histerids were aided in this destruction by the ants. Similar behavior in a natural bivouac could initiate or encourage considerable cannibalism.

Pulvinister nevermanni seemed to be groomed by ants more frequently than the *Euxenister* spp. The workers licked this histerid when it was hanging under the head or over the gaster of an ant, frequently licked so vigorously that the beetles were dislodged. Licking was concentrated on the pronotum and elytra and was most vigorous after the beetles emerged following a period buried in the dirt.

Pulvinister nevermanni flew more readily than *Euxenister* spp., many times hitting the glass covers of nests. The histerid usually took flight when first introduced into the nests, never after settling with the ants.

On one occasion, the glass cover was accidently knocked off a nest containing 4 *Pulvinister* partially buried in a small pile of brood in the center of the nest. As the glass moved, the ants became excited, picked up the brood, and began to run in a circle. Two histerids immediately rode on larvae, one rode on the gaster of an intermediate worker; and one rode on a minor's head. As long as the ants did not move their brood, the histerids did not fasten themselves to the ants or brood. This behavior probably prevents *Pulvinister nevermanni* from being left behind when the ants emigrate, but it is not known whether an alarm substance from the ants, mechanical disturbance, or the visual stimulus of the movement triggers the response.

Pulvinister nevermanni is associated only with *E. hamatum* and it was thought that the histerid would be attracted to the odor of its host. Five majors of both *E. burchelli* and *E. hamatum* were placed in several nests with 2 *Pulvinister* each but the histerids rode equally on both species of army ants. In other similar tests I was unable to discern any preference by *Pulvinister* for its specific host ants in the laboratory.

Discussion and Summary

Euxenister and *Pulvinister* are closely associated with specific ant hosts. All histerids collected from emigration columns were taken when brood was being carried and ant traffic was heaviest. None were collected in raid columns or in refuse deposits. *Euxenister* rode on booty and large army ant larvae, or walked in columns. Although histerids were rarely carried in the mandibles of ants, *Pulvinister* sometimes rode in a position between the mandibles of major workers, giving the appearance of being carried. *Pulvinister* rode on the army ant brood when larvae were large.

Histerids were less abundant as compared to some myrmecophiles such as Staphylinidae, but most colonies had at least one. *Euxenister wheeleri* was the most abundant histerid.

All three histerids are host specific and seem closely integrated with their host ant. In laboratory nests the histerids can survive up to 2½ months with non-host ants, never being accepted, but living on the fringe. The histerids can follow the trail pheromone of their host and probably also use other pheromones secreted by the ants. Probably dependence upon chemical communication systems of their host makes these histerids host specific.

No one knows where immature stages of these histerids develop. Most probably their life cycle is synchronized with the nomadic-statary phases of army ants. One histerid larva found in a laboratory nest

containing both *Euxenister wheeleri* and *Pulvinister* could not be determined to genus. Several attempts to find the immatures by digging up statary colonies and sorting the ants yielded no immatures. If immature growth can be completed in the statary phase, the newly-emerged histerids could leave with the ants when they emigrate. In the event the developing histerids emerge after the ants have gone, the histerid might follow the ants' chemical trail to the bivouac. However, when marked histerids were released on emigration trails from one to three days old the histerids had great difficulty in following the route and it took them several hours to go 3 meters. They were never collected in the colony when it was watched on subsequent nights. Since the histerids seem unable to use trails to find their host, it appears more likely the histerids locate their host by odor and fly to the bivouac.

Euxenister and *Pulvinister* are predators on army ant brood, all three species groom the ants to varying degrees, and all rub the ants and then themselves; probably to transfer the odor of the ants to their own bodies in order to integrate into the colony more easily. All will ride on army ant brood when it is large or on large pieces of booty. When the ants do not have booty and the brood is small, *Euxenister* usually walks in the columns, but *Pulvinister* ordinarily rides between the mandibles of majors. None of the histerids has true trichomes.

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